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THE GENUS RUPPIA L.

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URING AN ATTEMPT to find suitable plants to demonstrate the influence of temperature on their growth, differentiation, and persistence, attention was attracted to those of aquatic habitats, since of the two most essential climatic variables, temperature and moisture, moisture is constant. The marine algae and the marine spermatophytes have lent themselves particularly well to experimentation and some attention has been paid to each group. Of spermatophytes which pass their entire life history submerged, Zostera and Ruppia are two of those best suited for study. Zostera was found to be well adapted for observation in the open (see Setchell, Univ. Calif. Pub. Bot., 14:389-452, text fig. 59, 1929), and Ruppia for observation both in the open and in culture (see Setchell, Proc. Nation, Acad. Sci., 10:286-288, 1924). Ruppia is a rather delicate aquatic, without woody tissue of any appreciable amount, with little vegetative storage of starch or proteins, appearing and disappearing according to variation in conditions of habitat, seemingly likely to be fundamentally and quickly affected by changes of temperature and salinity, easy of culture, and offering opportunity of being used as a laboratory plant for the study of the influences of environmental factors.

It grows as a rule in shallow brackish water. The habitats vary from maritime, and therefore coastal, to interior saline springs, pools, and lakes. In many ways it resembles in general habit its near relative, Zannichellia palus-

tris L. It is called here by the common name of "Ditch Grass," in England as "Tassel Grass," but few except botanists are aware of its existence.

Linnaeus described the genus Ruppia in the Genera Plantarum of 1737, referring to Micheli's plate 35 of Buccaferrea maritima foliis minus acutis (1729, Nova plantarum genera), which he quotes, indicating by a cross (×) placed after the generic name, that he had seen, at that time, only a dried specimen. Since there are discrepancies of detail between the only specimen in his herbarium, labeled "l. maritima" in his own handwriting (!) (see Plate 47), and the plate of Micheli, we may suspect that the herbarium specimen was acquired later. We may conclude that the plate of Micheli clearly represents his conception of both genus and the type species. This specimen has a short, nonspiral peduncle. Linnaeus had in his herbarium another specimen which he labeled "Ruppia spiralis," which has an elongated, spiral peduncle, probably added to his collection later than the R. maritima.

Linnaeus, in 1737, published the Hortus Cliffortianus. He mentions Ruppia and under it has 2 series; first, among other citations he lists Micheli's Buccaferrea maritima, foliis acutissimis; and in the second he lists Buccaferrea maritima, foliis minus acutis, pl. 35, p. 72. He also indicates that he had collected a specimen near Leyden and had therefore become acquainted with the living plant. Linnaeus had not, at the time of the publication of the Hortus Cliffortianus, published his idea of varieties under species, but because of his arrangement it may be thought that he considered the two "species" of Micheli to be only varieties of one. Linnaeus does not name the second one.

In the first edition of the Species Plantarum, Linnaeus simply refers to "Buccaferrea maritima, foliis acutissimis Micheli, Gen., 72, t. 35, and seemingly unites the two "species" of Micheli. The idea of possibly two species of Ruppia, distinguished to some extent at least by the differing tips of the leaves, occurs several times in the later literature and perhaps most strongly in Hagström (Botan, Notis., 1911, 137) where his idea of Ruppia maritima and R. spiralis is expressed thus: "This has obtuse leaves and that acute." In other words, the Ruppia maritima of Linnaeus (in sensu strict.) has acute leaves, corresponding to the "foliis acutissimis" of Micheli, while R. spiralis has obtuse leaves, thus corresponding to the "foliis minus acutis" of Micheli. Micheli's figures on plate 35, which are really the type of the genus Ruppia, and therefore presumably the Ruppia maritima of Linnaeus, show short, noncoiled peduncles, so that the citation of "foliis acutissimis" by Linnaeus in the "Species" is misleading. Linnaeus, however, through the several editions of his "Genera," both in description and also by the specimen in his herbarium, suspected as having been collected on the "Westgota Resa," labeled (by him!) as Ruppia maritima (Pl. 47, gives evidence that the short, nonspiral form was the type both of his genus and of his species. The occurrence of a long-spiral, pedunculate form in his herbarium, labeled (by him!) "Ruppia spiralis" (Pl. 48), still further emphasizes this idea. The two specimens in Herb. Linn. are reproduced in this paper. Linnaeus then, in his herbarium,

really recognized two species, Ruppia maritima L. (Spec. Pl., ed. 1, 127, 1753) and Ruppia spiralis L. (in herb.), which was later published by Dumortier.

About 25 species have been proposed in Ruppia by taxonomists and almost all of them have been reduced to varieties or forms of R. maritima. The chief troubles have concerned themselves in the first place with the lack of realization among both earlier and later writers of the fact that Ruppia is dichogamous (see Ascherson, Bot. Zeit., 1871, p. 28, and in Engler u. Prantl, Natl. Pfl. Fam., II, 1:199, 1889), with proterandry; in the second place, with the confusion of the types of peduncles, and nature of pollination; in the third place, the ecophenic variable as to length of both peduncle and podogyne, even in the same plant; in the fourth place, varying persistence and robustness of the vegetative parts; in the fifth place, the variability in size and relative obliquity in the maturing fruits, the varying behavior of stigma and rostrum; and finally in the relation of robust and slim fruits so commonly found in the same inflorescence. The tendencies to recognize only one species, two species, or several species of the genus have been influenced by these considerations.

After Linnaeus, botanists seemingly regarded both series of forms as states or stages of one another. Botanists, such as C. A. Agardh (1823), W. D. J. Koch (1823, 1824), and others, began to split the Linnaean species, regarding, however, the *spiralis* form as the type. Dumortier (in 1827), to avoid confusion, published the name *Ruppia spiralis*. From then on some authors have applied this name to the spiral, peduncled form, but the majority have insisted, in spite of the evidence of the record, that this is the type of *R. maritima* L., and that the short, peduncled var. *rostrata* C. Ag. (*R. rostellata* Koch) is a variety of it. Fernald and Wiegand (Rhodora, 16, 1914, p. 121) adopt this interpretation of *R. maritima*. Hagström (*loc. cit.*, 1911, pp. 137, 138) recognizes the true *R. maritima* as distinct from the true *R. spiralis*.

Ascherson and Graebner (Synopsis, 1907, pp. 142–145) recognize one species, *Ruppia maritima* L., consisting of two subspecies, *A. spiralis* L. Herb., Dumort. and *B. rostellata* Koch.

As a result of our studies, it seems best to recognize two species, Ruppia maritima L. (1763) with short, nonspiral peduncles (the R. maritima var. rostrata of my earlier, 1924, preliminary account), and R. spiralis Dumort. (1827) with elongated, spiral peduncles (the R. longipes Fernald and Wiegand, non Hagström).

These conclusions were arrived at by an extensive study undertaken by myself, with the assistance of several graduate students, of the representatives of the genus as they occur in nature in the marshes around San Francisco Bay, and by culturing plants from these and many other localities.

Our cultures were established in beakers of 3 liter capacity. Into each beaker was placed about 100 grams of garden soil and 2.5 liters of water from the taps of the Berkeley water supply. In such cultures cuttings of rhizomes or seeds were planted. The beaker was covered with ordinary glass to prevent evaporation, and the plants grew and flourished, some of them for several

years without change of water or soil. Fresh tap water had to be added from time to time, in small quantities, to make up for the slight evaporation. A few cultures were made with natural spring water, with distilled water, and with potassium nitrate or magnesium sulphate added. In the two latter cases the plants grew without soil. Under favorable conditions, cultures from seed produced seeds in 60–80 days.

Ruppia plants, of both types of peduncle, were studied for about 15 years, both from certain localities more or less readily accessible and in cultures. The gross morphology of both types of Ruppia was studied in all stages from germination to fruit production, particular attention being paid to such uncertain matters as possession or absence of a primary root, types of peduncles, variations in fruit shape, and varying lengths of peduncles and podogynes. The definite discontinuity of the two types of peduncle is maintained. The ever-varying characters of fruits, podogynes, and peduncles may be expressed very differently on the same individual.

From the foregoing studies it is concluded that out of the many described species, there are two valid species in the genus, and that the various species, subspecies, varieties, proles, and forms which have been described are only reversible ecophenic, probably quantitative expressions of form and size. Persistence in the habitat is due to a continuation of conditions favorable to development. Ruppia plants are delicate in response to habitat and store little starch or other nutrient materials. In culture they live on indefinitely, but in their native habitats they may be short seasonal plants or longer or shorter lived perennials.

My sincerest thanks are due the Linnaean Society of London for permission to study and photograph the specimens of *Ruppia* in the Herbarium of Linnaeus.

PLATES

PLATE 47

Specimen of Ruppia maritima L. Herb. Linn., Genus 175. Sheet 1.

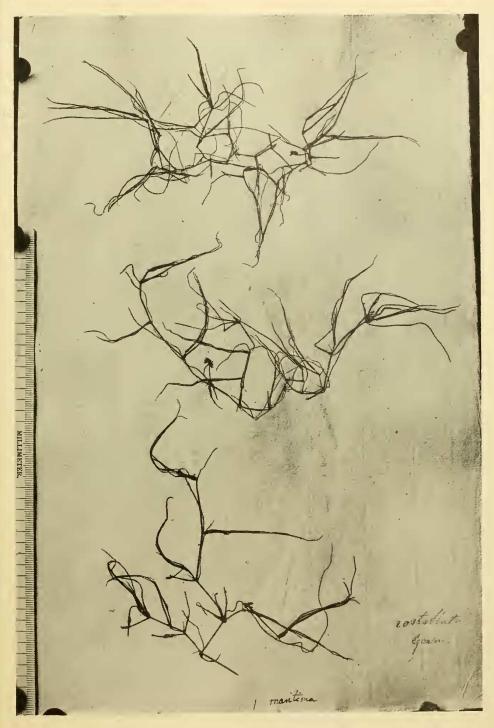


PLATE 48

Specimen of Ruppia maritima L. Herb. Linn., Genus 175. Sheet 2.

